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A Comparison of Aspects of the Biology of *Paranemertes peregrina* (Nemertea) from Bodega Harbor, California, and Washington State[1]

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ABSTRACT: In Bodega Harbor, California, the nemertean *Paranemertes peregrina* spawns in June or July. Adults in the study area were small in comparison to worms found on two Washington mud flats. Population density of active worms averaged 7.38 worms/m^2, with much variation due to time of day of low tides. Approximately 28 percent of the active population ate during the low tide periods that were sampled. Prey included spionids, nephtyids, polychaetes with capillary setae, and syllids (in decreasing importance). The number of prey families in the diet of California nemerteans was higher than in the two Washington mud flat populations and preferred nereid prey was less abundant in California and comprised less of the total diet of nemerteans there. Spionids were the major prey of California nemerteans in spring and summer; nereids were the major prey in fall and winter. In food preference tests, nemerteans showed negative responses to phoronids and lumbrinerids and positive responses to *Nephtys caecoides*. In comparison to three Washington populations, the population in Bodega Harbor was most similar to a rocky intertidal population and much different from two mud flat populations.

THE PREDATORY NEMERTEAN *Paranemertes peregrina* occurs in various habitats along the Pacific coast of North America from Ensenada, Mexico, through the Aleutian and Commander Islands (Coe 1940), and in Japan (Yamaoka 1940). Life history and feeding biology of this nemertean were studied in both rocky and mud flat intertidal habitats in Washington State (Roe 1971, 1976). The present observations concern aspects of life history and feeding biology of *P. peregrina* in a more southern habitat at Bodega Harbor, California; and comparisons are made of Washington and California populations of *P. peregrina*.

MATERIALS AND METHODS

Nemerteans were observed in and collected from the mud flat in the Bodega Marine Laboratory preserve in Bodega Harbor, California. Most worms were counted and collected along the edges of a low area that contained water even during low tide. The area was comprised of sandy mud and became quite hard and dry during low tides except in low places where water remained. *Ulva* and *Entermorpha* spp. were present most of the year in low places, but the major portion of the mud flat was bare most of the year. The mud flat was superficially similar to both mud flat areas studied in Washington in sediment and in animals and plants living on and in it.

Densities of active *Paranemertes peregrina* were determined by counting numbers per square meter in each square meter along a 25-m transect laid along the edge of the low area described above. For estimates of size and sex of the worms through time and study of food of the worms, 50 worms from the area were collected during each sampling period. Each of the 50 worms was isolated in a small jar containing clean seawater and was kept near 15°C for at least 48 hr. Then length and width of each worm was mea-

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sured as it crawled along the bottom of a white enamel pan. Sex was determined if gametes could be seen through the ventral ivory-colored epidermis. Any debris in the jar was placed on a microscope slide and searched for polychaete setae or any other food remains.

Jars with 7.4-cm diameter openings were inverted over the center of square meter areas along the transect, and mud to about 7–8-cm depths under the jar was collected. Later, the mud samples were sorted and inhabitants were identified and counted. This provided a general knowledge of what prey organisms occurred and allowed estimates of densities of some of the more abundant prey. However, spionids, a major prey, were usually not found by this method as they need to be preserved and sieved with a 0.5–1.0-mm-mesh sieve to be adequately sampled (J. Oliver, Moss Landing Marine Laboratories, personal communication; Knox 1977). Since many prey in these samples were used as experimental prey, the mud was not preserved.

Behavior of nemerteans and various possible prey were observed both in nature and in the laboratory with respect to feeding biology and escape responses. Experiments consisted of placing a prey or part of a prey directly in front of a nemertean and observing the response of both. Responses of nemerteans were recorded as negative if the worm did not react or reacted by backing or crawling away. Responses were considered positive if the nemertean everted its proboscis onto the prey or if it tried to eat the prey. Controls (i.e., nereid prey to which *Paranemertes peregrina* nearly always reacts positively; see Roe 1970) were not used.

RESULTS

Paranemertes peregrina at Bodega Harbor had a discrete spawning period during summer months. In June 1975, males comprised 18 percent of the animals collected and females 28 percent; in June 1976, males equaled 10.3 percent and females 15.4 percent. In July 1975, males and females each comprised 4 percent of the population; and in July 1976, males and females were each 13.2 percent of the population. A few sexually identifiable animals were also found in April 1975 and September 1976. Spawning periods of Washington worms were: Edmonds rocky area, March and April; Garrison Bay mud flat, April and November; Snug Harbor mud flat, June and November (Roe 1976). Tiny, pale worms identified as juveniles were apparent in the population in October. By January they had grown darker and could not be distinguished from older animals. The average size (area) of the worms and the population composition each month can be seen in Table 1. California animals were small compared to worms from Washington mud flats and the California population most closely resembled the rocky intertidal population from Washington in sizes of individuals (see also Roe 1971, 1976).

Overall population density of active California worms was 7.38 worms/m^2. There was much variation in densities due to time of day and weather conditions. Densities ranged from a high of 20.6 worms/m^2 before sun-up in June 1976, to so few that only 12 worms were seen in approximately 60 m^2 during an afternoon low tide in November 1975, when the sun was shining brightly. The time of day of the low tide apparently was the most important physical variable determining the activity periods of the worms, with few worms active during sunny afternoon low tides and many active during nighttime low tides. For example, approximately 30 animals were seen over a 1/4-mile stretch across the mud flat during an afternoon low tide. However, about 30 min after dark, over 20 worms were counted in 1 m^2 of the same area in a very short period of time and many other 1 m^2 sections contained approximately as many worms. Other weather conditions influenced the number of active worms or how long individuals remained active during a tide but appeared to be less important than day versus night. For example, once winds

TABLE 1

Average Sizes (mm², ± 1 SD) of *Paranemertes peregrina* in Bodega Harbor and Washington for Selected Months

Month and Year		Location			
		Bodega Harbor, California, mud flat	Edmonds, Washington, rocky area	Garrison Bay, Washington, mud flat	Snug Harbor, Washington, mud flat
June	1969		71.7 ± 34.2	196.2 ± 93.9	232.0 ± 94.7
	1975	104.5 ± 45.2			
	1976	53.8 ± 26.4			
July	1975	70.6 ± 45.8			
	1976	109.4 ± 87.2			
Sept.	1968		97.7 ± 38.5	187.0 ± 107.0	122.9 ± 74.3
	1975	54.6 ± 27.4			
	1976	37.6 ± 20.8			
Nov.	1975	57.6 ± 19.6			
Dec.	1975	77.0 ± 53.4			
Jan.	1969		93.2 ± 45.7	207.8 ± 81.1	130.2 ± 63.2
	1976	50.5 ± 24.8			
Feb.	1977	107.6 ± 71.6			
Apr.	1968			138.7 ± 83.0	
	1969		70.1 ± 49.1		155.9 ± 97.9
	1975	123.8 ± 46.6			
	1976	76.9 ± 43.1			

were gusting to 48 mph. Almost no worms were out on the drier parts of the mud flat, but many were active in every small wet depression and the density was a normal 7.3 worms/m^2.

On the average, 28 percent of the active members of the Bodega Harbor population ate per low tide period, with a low of 4 percent and a high of 51.3 percent. (In the Washington populations the percentages of active animals that ate per low tide were: Edmonds rocky area, 38.6 percent; Garrison Bay, 30.5 percent; Snug Harbor, 42.8 percent; Roe 1976.) An important factor determining the number of animals that had eaten just prior to being collected was the length of time the animal had been active before being collected. *Paranemertes peregrina* feeds at low tide, emerging from its burrow shortly after water recedes from the mud as the tide is going out, and in Washington it took about 45 min for a nemertean to find a prey item (Roe 1976). At Bodega Harbor the few worms seen during one low tide before dark were collected; of these, 32.1 percent (9 of 28) had fed. After dark, about 50 min later, when many worms had been active for 15–30 min, only 4 percent (1 of 20) of the animals collected had eaten.

At Bodega Harbor polychaete prey included spionids, primarily *Pseudopolydora paucibranchiata* (42.47 percent of the total diet); nereids, primarily *Platynereis bicanaliculata* (29.45 percent of the diet); the nephtyid *Nephtys caecoides* (17.12 percent of the diet); and a few individuals of the syllid *Exogone lourei* (1.37 percent of the diet). Capillary setae were the only setae found in 9.59 percent of the samples. They were not identified further.

Paranemertes peregrina at Bodega Harbor showed a strong seasonal difference in major prey consumed. Spionids were the major prey in spring and summer months (Apr. 1975 = 28.6 percent, Apr. 1976 = 81.2 percent, June 1975 = 25 percent, June 1976 = 90.5 percent, July 1975 = 100 percent, July 1976 = 70 percent, Oct. 1975 = 6.25 percent, Nov. 1975 = 0 percent, Dec. 1975

TABLE 2

NUMBER OF PREY FAMILIES IN THE DIET OF *Paranemertes peregrina*, PROPORTION OF THE DIET THAT WAS NEREIDS, AND ABUNDANCE OF NEREIDS IN THE HABITAT (FOUR LOCATIONS)

	BODEGA HARBOR, CALIFORNIA, MUD FLAT	EDMONDS, WASHINGTON, ROCKY AREA*	GARRISON BAY, WASHINGTON, MUD FLAT*	SNUG HARBOR, WASHINGTON, MUD FLAT*
Number of prey families	4–5	5	4	3
Nereid proportion of diet (%)	29.5	4.4	76.0	89.3
Number of nereids/m^2 (annual average)	487–504	28	819	3,240

*Data for Washington populations from Roe (1976).

= 5.56 percent, Jan. 1976 = 20 percent, Sept. 1976 = 0 percent, Feb. 1977 = 0 percent) and nereids were the major prey in fall and winter (Apr. 1975 = 64.3 percent, Apr. 1976 = 6.25 percent, June 1975 = 25 percent, June 1976 = 0 percent, July 1975 = 0 percent, July 1976 = 0 percent, Oct. 1975 = 18.75 percent, Nov. 1975 = 75 percent, Dec. 1975 = 66.7 percent, Jan. 1976 = 40 percent, Sept. 1976 = 100 percent, Feb. 1977 = 20 percent). Nephtyid prey did not show strong seasonality although in general more were eaten in fall and winter. Syllids were eaten in June and July. In Washington populations spionids were primarily eaten in fall and winter (Roe 1976).

Although few small samples of Bodega Harbor mud were searched for prey, relative abundances of major prey species could be determined. *Platynereis bicanaliculata* was most common in fall, being the most abundant of all prey species in samples from September (18 in four samples, or 1023/m^2), October ("several" in a nonquantified sample), and November (50 in six samples, or 2274/m^2). Only two other individuals were found in the prey samples—one in February and one in April. From these data it was estimated that an average of 487.2–503.5 nereids/m^2 occurred annually. In fall all nereids were juveniles, with an average length of 8.95 mm in October. Nephtyids were less abundant but were found more consistently: June, two (nonquantified sample); October, one (nonquantified sample); November, six in five samples; April, one in three samples. *Exogone lourei* was most abundant in June and July: two in ten samples in June 1975; two in 20 samples in June 1976; one in July; and one in a nonquantified sample in October. Spionid abundances were underestimated in the sampling technique employed. However, *Pseudopolydora paucibranchiata* is listed as "abundant" (subjective comparative estimate of the authors) in Standing, Browning, and Speth (1975). (For comparison, *Platynereis bicanaliculata* is also listed as "abundant" and *Nephtys caecoides* as "common to abundant" in that publication.)

The number of prey families of nemerteans at Bodega Harbor was higher than that in the two Washington mud flat populations and the proportion of preferred nereid food in the diet was less, as was density of nereids in the California mud flat (Table 2).

In laboratory and field experiments on the feeding behavior of Bodega Harbor *Paranemertes peregrina*, individuals showed no response or negative response to *Phoronopsis viridis* in 57 of 58 experiments. Only once did a nemertean evert its proboscis, and on that one occasion, the proboscis was everted only a short distance and was not wrapped around the phoronid. In places where *Phoronopsis viridis* was abundant, 157 nemerteans were observed in close proximity to the phoronids with no response on the part of either species.

In 55 feeding experiments with *Lumbrineris zonata* as prey, 54 were negative. In the one positive trial, the nemertean everted its proboscis about 1 cm but did not touch the lumbrinerid. Then the nemertean crawled next to the annelid but did not try to feed. The only association of nemerteans and lumbrinerids seen in the field showed that although the worms were in contact, there was no attempt to eat the polychaete.

In experiments with *Nephtys caecoides* as prey, responses were recorded as negative in 12 of 18 trials. However, in four of these 12 the nemertean jerked back strongly upon contact with the nephtyid and continued to jerk back, a definite sign of recognition (Roe 1970). In the other six trials, the nemertean everted the proboscis over the nephtyid at least once and usually several times, and in five of the six trials the nemertean ate or tried to eat the polychaete. In nature, *Paranemertes peregrina* was observed while eating nephtyids five separate times.

Of the prey tested, nephtyids were the only ones to show strong escape responses. Upon contact with the nemertean proboscis, nephtyids would try to burrow. Their speed in burrowing was greatly reduced, however, probably due to the nemertean toxin. They were also observed to spread their setae and parapodia, making themselves larger and more bristly. Since they were often large enough to make feeding by *Paranemertes peregrina* difficult (the nemertean was unable to ingest the nephtyid in three of the six food preference trials), this increase in diameter would be an effective escape mechanism.

DISCUSSION

The *Paranemertes peregrina* population living in the mud flat at Bodega Harbor, California, differed in several life history aspects from populations of this species living in two similar intertidal mud flat areas and at a rocky intertidal area in Washington State (Roe 1976). The spawning period of *P. peregrina* at Bodega Harbor occurred later in the summer (June–July) than did the spawning seasons of the Washington populations (March, April, and June). On the mud flats in Washington, reproductively ripe worms could also be found in the fall, whereas at Bodega Harbor, reproduction appeared to be restricted to summer. In this respect the Bodega Harbor population was similar to the Washington rocky intertidal population, which also had one discrete reproductive reason per year. The worms at Bodega Harbor appeared to be smaller than those of the Washington mud flats, again being similar to the rocky intertidal Washington population (see also Figures 3, 4, 5 in Roe 1971).

The Bodega Harbor nemerteans were much more nocturnal in their activities than were the Washington worms. Few animals were active at the Garrison Bay, Washington, mud flat in afternoon tides in spring (Roe 1976), but otherwise animals could be found during most low tides. The Bodega Harbor population, in contrast, showed strikingly different behaviors within 30 min after the sun came up or went down, most animals being active only during darkness. Black-bellied plovers winter at Bodega Bay and have been observed to eat *Paranemertes peregrina* (L. Stenzel, Point Reyes Bird Observatory, personal communication). This predation at Bodega Harbor, which is absent most of the year in Washington, may be a reason for the nocturnal activity of *P. peregrina* at Bodega Harbor, but there is no evidence to support this hypothesis at present, nor is there knowledge of any other such observations.

The Bodega Harbor population ate similar prey to the Washington populations, with nereids and spionids being major foods for all populations, although the seasonality of the spionid component of the diet was reversed. In California spionids were eaten primarily in spring and summer; all three Washington populations ate spionids mainly in fall and winter. Also, spionids were the dominant prey of the Bodega Harbor population, comprising nearly 43 percent of the diet. In Washington, the two mud flat populations ate mainly nereids although at the rocky area where nereids were not abundant, spionids were again 43 percent of the diet (Roe 1976). Although *Nephtys caeca* was present on the Washington mud flats, it was not common (Woodin 1972) and it was not found in fecal analysis from any Washington nemerteans. At Bodega Harbor *N. caecoides* comprised 17 percent of the nemertean diet and also showed an escape response to *P. peregrina*. The type of prey, however, was similar in all habitats. *Paranemertes peregrina* eats errant polychaetes or ones that have shallow or wide burrows or tubes.

Common polychaetes, such as lumbrinerids, maldanids, and capitellids, that have long narrow bodies and live in long narrow tubes are typically not recognized by *Paranemertes peregrina* as prey. Tom Ronan (University of California, Los Angeles, personal communication) occasionally saw a *P. peregrina* eating a lumbrinerid at Bodega Harbor. However, these were always instances when the lumbrinerid was on the surface of the mud, not in its burrow. Likewise, Ronan occasionally (about once per 1000 phoronids) found a *P. peregrina* down a tube of *Phoronis viridis* with part of the phoronid missing. Ronan assumed the nemertean was eating the phoronid, although he never actually saw feeding. Experiments on feeding behavior and escape responses done during this study suggest that *P. peregrina* rarely reacts to phoronids or lumbrinerids as prey and that phoronids do not respond to the presence of nemerteans with escape responses (escape responses of lumbrinerids were not tested). Lumbrinerids and phoronids could be rare food items in the nemertean diet, but they are not frequently consumed.

Optional foraging strategies suggest that as the abundance of a preferred food type [nereids, Roe (1970, plus further observations)] in the diet increases, the number of less preferred food items in the diet should decrease, or increasing food abundance should lead to greater food specialization (Pyke, Pulliam, and Charnov 1977). Studies of *Paranemertes peregrina* in habitats with differing abundances of nereid prey show clearly that this nemertean becomes more of a food specialist with increasing abundances of preferred prey and food specialization decreases with reduction in numbers of preferred prey. The Bodega Harbor population shows many similarities to the rocky intertidal population in Washington and some to the Garrison Bay mud flat population, especially with respect to dietary diversity. The nereid density at the Bodega Harbor study site was also greater than that at the rocky Washington area but less than that at Garrison Bay (Table 2).

This study showed that populations living approximately 1000 miles distant from one another were more similar to each other than were populations living about 65 miles from each other, especially with respect to feeding behaviors. It is suggested that animals often respond to local conditions such as prey abundance, and that latitudinal differences may be due more to local influences than to large overall differences associated with latitudinal gradients.

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